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Lesser Black-backed Gulls *Larus fuscus* thriving on a non-marine diet

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ABSTRACT

Capsule: Lesser Black-backed Gulls *Larus fuscus* breeding 30 km from the coast in the Netherlands focussed entirely on terrestrial food sources and reached relatively high breeding success.

Aim: To gain insight in the foraging ecology, habitat use and breeding performance of inland-breeding Lesser Black-backed Gulls.

Methods: We received data from seven birds fitted with global positioning system (GPS) loggers. The colony was frequently visited to collect pellets and boluses and to monitor reproductive success, mortality and growth rate of chicks.

Results: The GPS data revealed that mainly terrestrial habitats were used, 98% of these GPS positions were within 25 km of the colony. Refuse dumps were the most preferred sites, but also agricultural fields and freshwater bodies were often visited. Only two of the 710 recorded trips were directed to the North Sea. The pellet and bolus analyses confirmed the GPS data: no marine food remains were found. Breeding success of birds in the enclosure was relatively high, with 90% of eggs hatched and 51% of chicks fledged (1.6 chicks/pair).

Conclusions: Relying on terrestrial food is feasible when sources are available in the vicinity of the colony. We conclude that Lesser Black-backed Gulls could theoretically shift towards inland breeding after a fishery discards ban.

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Large gulls *Laridae*, among them the Lesser Black-backed Gull *Larus fuscus*, are considered to be generalists in their selection of prey (Harris 1965, Cramp & Simmons 1978, Kubetzki & Garthe 2003, Camphuysen 2013). In most coastal colonies around the North Sea, however, Lesser Black-backed Gulls are primarily marine-orientated, conducting long foraging flights offshore and feeding both on discards of fishing vessels as well as on natural fish prey (Furness *et al.* 1992, Camphuysen 1995, Garthe *et al.* 1996, Camphuysen 2013).

Many coastal colonies in the dune area of the mainland North Sea coast of the Netherlands were abandoned due to predation pressure by Red Foxes *Vulpes vulpes* (Spaans 1998a). Consequently, Lesser Black-backed Gulls in the Netherlands started to colonize areas farther inland (especially in the Delta area in the south-western part of the Netherlands), and the number of birds breeding inland has been increasing ever since (Camphuysen 2013). However, the largest colonies of this species and the majority of the Dutch breeding population are still located at the coast (van der Helm 1992, Spaans 1998b, Camphuysen 2013).

In terms of reproductive output, foraging at the open sea was shown to be advantageous compared with feeding on land for this species and other Larids (Annett & Pierotti 1989, Spaans *et al.* 1994, Bukacinska *et al.* 1996). The energetic quality of fish is relatively high, assuring a high reproductive performance when consumed in sufficient quantity and quality in the breeding period (Garthe *et al.* 1996, Camphuysen 2013). Therefore, it has been assumed that the inland distribution of gulls is limited by the distance to accessible fish prey (Hüppop & Hüppop 1999).

However, a recently accepted European Union ban on discards (European Parliament 2013) is expected to diminish the offshore feeding opportunities of large gulls (stepwise from 2014 onwards), which will likely reduce the food availability in the marine environment and cause a shift in diet (Bicknell *et al.* 2013). Lesser Black-backed Gulls can readily switch to terrestrial food resources (Oro 1996) and recent studies showed that there is a large inter-annual, inter-individual and even within-week variation in foraging destinations between terrestrial and marine sites at coastal colonies

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(Thaxter *et al.* 2015). Also inland-breeding birds in the Netherlands are known to exploit alternative terrestrial food sources extensively (Spaans 1998b, Camphuysen *et al.* 2005). Nevertheless, despite the increasing number of inland Lesser Black-backed Gulls colonies in the Netherlands, there have been few field studies on them. Studies on food choice, habitat use and corresponding reproductive output have mainly been studied in coastal colonies.

In order to gain insight in the foraging site selection, diet and corresponding reproductive performance of Lesser Black-backed Gulls breeding in a non-coastal colony, we conducted our study in a colony in Lake Volkerak, The Netherlands, situated approximately 30 km from the North Sea. The research was carried out within the framework of the Shortlist Masterplan of Rijkswaterstaat Waterdienst and Rijkswaterstaat Directie Noordzee to gather relevant ecological data on, for example, foraging ranges, flight heights, activity patterns, proportion of floaters (i.e. sexually mature but not yet breeding individuals) in the population, and figures on annual survival, especially for the fraction of birds that forage offshore and can potentially be impacted by future windfarm developments. The study was based on global positioning system (GPS)-tracking and pellet analysis, and was extended by an enclosure study to reveal the reproductive performance that birds could achieve by their foraging decisions.

Materials and methods

Study site

Lake Volkerak, together with Lake Krammer (with a total surface area of 6450 ha) is a former arm of the North Sea, which was closed off in 1987 and became a freshwater lake. Lesser Black-backed Gulls breed at five different sites within the lake (Strucker *et al.* 2011). Our study focused on the colony at the Noordplaat (N51.644029°, E4.237396°), a group of three islands with a surface area of 13 ha. As part of the management plan, vegetation is systematically removed from a strip of 15–50 m at the western and southern side of the most western island, in order to prevent plant succession and preserve the Lesser Black-backed Gull colony. In 2010, 41 pairs of Lesser Black-backed Gulls, 18 pairs of Herring Gulls *Larus argentatus* and 112 pairs of Barnacle Geese *Branta leucopsis* bred on the Noordplaat (Strucker *et al.* 2011).

Data collection and analysis

Breeding ecology

In 2010, in the colony on the Noordplaat, 40 nests (of which six turned out to be of Herring Gulls) were marked with wooden poles and their geographical position was recorded with a handheld Garmin GPS unit. During the breeding phase, 31 adult Lesser Black-backed Gulls were trapped on nests, using walk-in cages. Based on morphometric measurements and other phenotypic characteristics, birds were sexed (Muusse *et al.* 2011) and subsequently colour-ringed. On 18 May, an enclosure was built with 0.5 m high, 0.02 m mesh size chicken wire to fence off 18 nests (including eight nests of ringed birds) in the middle of the colony. The lower 0.4 m of the chicken wire was covered with green hard plastic to prevent chicks from forcing their head in the mesh and injuring themselves. The enclosure was subdivided into two sections (an eastern and western part) with roughly equal surface areas. There were 13 Lesser Black-backed Gull nests (comprising 32% of the whole colony) in the enclosure, with four nests in the western part (plus two Herring Gull nests), and nine nests in the eastern part (plus three Herring Gull nests).

The colony was visited twice a week (three to four days interval between two visits) between mid-May (breeding phase) and Mid-July (fledging of the last young) in 2010. Altogether 16 visits were made to the colony. During the visits, all marked nests on the island were assessed for the presence of eggs or chicks. Eggs were sequentially numbered with a permanent marker to record laying order, were weighed to the nearest 0.1 g, and length (L) and width (W) were measured to the nearest 0.001 m. Subsequently, egg volume (V) was calculated by the formula (Stonehouse 1966):

$$V = K_v * L * W^2,$$

where the constant K_v was set at 0.5035 (Camphuysen 2013). On the following visits, the pipping date (appearance of star-like bursts in the shell) and the actual hatching date of the eggs were recorded. Wet chicks were registered as hatchlings of that day; dry chicks were assigned to one of the previous days according to their size. As the incubation of eggs had already started by the first visit to the colony, median laying date in the colony was calculated by subtracting the documented incubation period of Lesser Black-backed Gulls (28 days: MacRoberts & MacRoberts 1972b, Camphuysen 2013) from the mean hatching date observed in the field.

Upon the first encounter, young chicks within the enclosure were temporarily marked with coloured cable ties. These were cut short so as not to get entangled in vegetation or the enclosure. When the tibias of the chicks were more developed, the cable ties were replaced by a permanent aluminium ring on the tarsus and a colour-ring on the tibia. During each visit, chick weight (to the nearest g), total head length (from the tip of the bill to the back of the head to the nearest 0.1 mm) and from the onset of feather growth also stretched wing length (from the bend of the wing to the tip of the longest primary to the nearest mm) were measured. In order to minimize disturbance to the colony, searching for chicks was terminated after 45 minutes, whether or not all individuals were found. Chicks missing before the age of 30 days were considered dead. Chicks seen in the enclosure at the age of 30 days but not afterwards were considered to be fledged.

In order to compare the fledging rate of chicks of treated adults (i.e. those ringed or equipped with GPS; see below) and a control group of the adults (not ringed or equipped with GPS) within the enclosure, the number of dead and fledged chicks was ordered in a two by two contingency table and a V-square statistic was carried out (a Chi-square test for small sample sizes). The fledging rates were also compared based on the number of hatched eggs and the number of chicks fledged. Dealing with dependent samples, this comparison was carried out using a McNemar chi-square test. All statistics of the study were carried out using SPSS 15.0 for Windows.

Dietary analysis

Boluses of partly digested stomach contents regurgitated during the handling of the adults or chicks were collected, labelled with the date, location and originating individual, and later kept frozen in the laboratory until further analysis. On nine days, pellets of regurgitated indigestible prey material were also collected in the enclosure. If applicable, the originating nest number was recorded, otherwise the appropriate enclosure side was recorded (east or west). There were no pellets collected in the immediate surroundings of Herring Gull nests. Nevertheless, Lesser Black-backed Gull and Herring Gull nests were in close vicinity of each other, and in most cases pellets could not be attributed to species.

Altogether 18 boluses and 67 pellets were collected, which were analysed under a 10x binocular magnification. Food remains were identified to species group or to species if possible. Subsequently, pellets and boluses were qualitatively ordered in the main categories of terrestrial, aquatic or mixed sources. Results are presented as frequency of occurrence (in percentages) of food items in pellets and boluses (Barrett *et al.* 2007).

Habitat use

Of the 31 birds trapped on nests, 9 birds (4 of them breeding within the enclosure) received an 18 g, solar-powered GPS logger, (UvA-BiTS, Bouten *et al.* 2013). The loggers were attached as backpacks with a flexible harness of synthetic elastic inner lining and teflon outer lining (Bally Ribbon Mills, USA). Loggers were only deployed on birds in good condition and with a minimum weight of 700 g. The system was set to obtain the geographical position twice per hour in May, four times per hour in June and again twice per hour afterwards. In addition, ground speed and altitude above sea level were also recorded. Data were automatically downloaded from the GPS devices via a wireless network to one of two antennas placed on the island. The antennas transmitted the data to a laptop that was also positioned on the island and powered by two solar panels. The laptop had a wireless Internet-connection, and thus data could be remotely downloaded and new configurations uploaded.

GPS logger 321 stopped working on the first day and logger 323 after one week (Table 2). Therefore, data analysis was restricted to seven GPS-transmitters (representing 8.5% of all birds in the colony). GPS measurements showed that a few birds were conducting only a few trips in the first two days after deployment. Therefore, in order to avoid biased data after the placement of the loggers, the first three days of tracking were excluded from the analysis. Visited destinations were qualitatively categorized based on publicly available satellite images. The position of the colony was specified as a 1 km (the approximate distance to the nearest shore of Lake Volkerak) radius circle around the centre of the colony, to include birds floating on the water around the island. A kernel density analysis on the measured GPS positions was conducted (Thaxter *et al.* 2015). Search radius to fit the kernel densities was 1.5 km and positions within a 1 km zone around the colony were excluded. The kernel density analysis was carried out using the Spatial Analyst Tools within ArcGIS 10.1. Based on the resulting kernel rasters, isopleths lines of 50%, 75% and 95% were extracted using the Geospatial Modelling Environment (version 0.7.2.1) to visualize where birds were found most often.

Results

Feeding ecology

Although most of the pellets comprised multiple food sources, in most cases a main category of origin could be identified. All in all, there were no food remains of marine origin found in the pellet or bolus samples. Both sample types indicated that the Lesser Black-backed Gulls mainly relied on terrestrial food sources. For example, most of the pellets (84%; Table 1, see an overview of all pellets in Supplementary Online Appendix 1) contained at least a small quantity of beetle remains.

Table 1. Source of origin of the pellets ($n = 67$). % of all pellets provides the main categorization of pellets into terrestrial, mixed and aquatic origin. Mixed source regards samples with both terrestrial and aquatic food remains within. Prey types occurring in the pellets are grouped per source of origin and provided in a descending order based on the percentage of occurrence in all pellets.

	% of all pellets	Prey type	Occurrence of prey type (%) within all pellets
Terrestrial	69	Beetles	84
		Mole	36
		Refuse	31
		Ants	28
		Seeds	27
		Bird remains	10
		Larvae	9
		Mouse	1
		Eggshell	1
Mixed	19	Shell remains	40
Aquatic	12	Freshwater fish	28
		Crustacea	10
		Zebra mussel	6

Table 2. Data transmission period and number of fledglings raised by Lesser Black-backed Gulls. Number of fledglings outside the enclosure could not reliably estimated (indicated by '–').

GPS-ID	Sex	Period GPS data	Number of fledglings
189	Male	22/5–11/7	2
299	Male	22/5–10/7	1
316	Female	22/5–8/6	0
322	Female	22/5–8/6	–
330	Male	22/5–16/6	–
331	Female	22/5–3/7	–
332	Male	22/5–11/7	–
[a]321	Male	22/5	2
[a]323	Female	22/5–29/5	–

[a]Due to technical problems these tags were not included in the analysis.

Based on the frequency of occurrence in pellets, Moles *Talpa europaea* also seemed to be important prey, occurring in 36% of all pellets. Furthermore, 31% of the pellets contained food remains from refuse dumps (indicated by a large amount of paper, glass, plastic or a mixture of these). The frequency of occurrence of human waste in pellets was low, however, compared with boluses: 61% of the boluses contained food remains of refuse dumps.

Regarding food items from undoubtedly aquatic sources, fish otoliths were found most often (in 28% of pellets; Table 1). All of these originated from freshwater fish, mostly from *Cyprinidae* species. Furthermore, 10% of the pellets contained remains of freshwater crayfish or crabs (Spiny-cheeked Crayfish *Orconectes limosus* and Chinese Mitten Crab *Eriocheir sinensis*), while another 6% contained shells of Zebra Mussels *Dreissena polymorpha*. Small pieces of shells from unknown species were, however, found in many more pellets (40%).

Eighty-three per cent of the boluses ($n = 18$) had a terrestrial origin. Only 11% was categorized as having a mixed origin and 6% as having an aquatic origin. Most of the boluses contained food items from domestic waste. Mainly bread or waste meat was encountered, for instance chicken skin or pure fat. In boluses, earthworms (on two occasions), leatherjackets (larvae of crane flies *Tipulidae* spp.) and a beetle species were also identifiable (Garden Chafer *Phyllopertha horticola*).

Habitat use

Altogether 710 foraging trips were identified. There were only two occasions (0.3% of all flights) when a bird flew to the North Sea. One of these trips (conducted by a female, ID 316) lasted only one hour, on 5 June 2014, during the chick-rearing phase. The bird had just lost its last chick around the time of this trip. A few days later data transition from this bird stopped (Table 2). Another female (ID 331), conducted a nearly day-long trip to the North Sea at the end of the chick-rearing phase, on 27 June. The farthest measured locations during this trip were 15–20 km away from the coast, with the farthest point being 64 km from the colony. After returning to land, the bird did not enter the colony but flew straight to the refuse dump of the town Bergen op Zoom. The last signal from this GPS logger was received a few days later (3 July; Table 2). The last egg in the nest of this individual was found on 22 June and on later visits the nest was empty.

All other foraging flights of Lesser Black-backed Gulls were directed inland, mostly to the south-southeast (Figure 1). Nearly all of these were directed to terrestrial foraging sites and only some to freshwater sites. Ninety-seven per cent of the measurements occurred at a distance less than 25 km from the colony. Fifty-one per cent of these points were in or around the colony at less than 1 km distance (Figure 2). A second peak (19% of all measurements) occurred between 15 and 20 km from the colony (Figure 2), corresponding to foraging locations in or nearby two towns (Bergen op Zoom and Roosendaal).

Individuals showed a high personal preference for specific foraging sites (Figure 1) while nearly completely neglecting sites that were frequented by other individuals. The main foraging sites included agricultural fields to the south-southeast of the colony (Figure 1, location 1, almost exclusively used by ID 332 and often visited by most of the birds), the town of Bergen op Zoom (Figure 1, location 2, visited by ID 316 and 330), a refuse dump near to Bergen op Zoom (Figure 1, location 3, almost exclusively used by IDs 189 and 331 and regularly by IDs 299, 316 and 322), the town of Roosendaal (Figure 1, location 4, visited by ID 299, 316 and 322). When Dutch refuse dumps were closed on Sundays, the birds

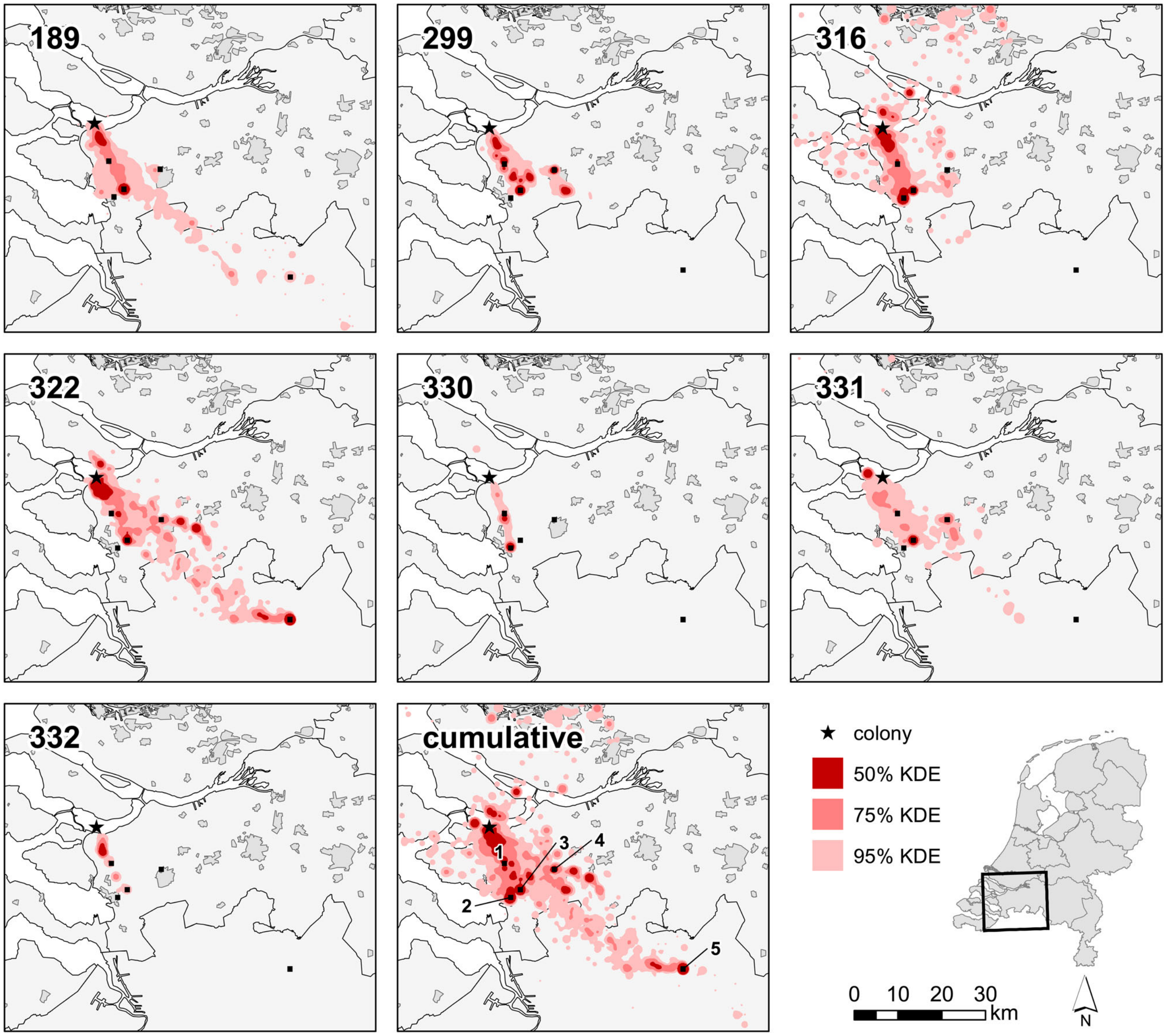

Figure 1. Kernel density estimates of space use by seven Lesser Black-backed Gulls and a cumulative map based on GPS measurements outside a 1 km zone around the colony (location depicted by a black star). Dark red areas provide the 50% kernel density estimates, clearly showing the individual preferences of the birds. The most important foraging areas are numbered: (1) Agricultural areas; (2) Town of Bergen op Zoom; (3) Refuse dump of Bergen op Zoom; (4) Town of Roosendaal and (5) Refuse dump in Belgium. Darker grey shaded areas are human settlements.

switched to alternative food sources, while one individual (ID 322) often flew farther to a Belgian refuse dump that was not covered up (Figure 1, location 5).

Breeding ecology

Quantification of hatching success outside the enclosure was not reliably possible (Table 3) because chicks could wander freely around and could not be confidently linked to a nest. Hatching of the eggs within the enclosure ($n = 36$) occurred in the period 22 May–4 June, with a median date of 28 May 2010. Considering an incubation period of 28 days, the calculated median laying date of these eggs was 1 May. Hatching success was high in the enclosure (94.2%): at least one egg hatched in each nest.

The first fledged chick left the enclosure on 25 June. The peak fledging period occurred in the first days of July. Fledging success of chicks within the enclosure was generally high (51%), resulting in a relatively high, 1.6 fledged young per nest (Table 3). The number of fledged young of the treated birds (ringed or GPS-tagged) was lower, but still relatively high (1.3 fledged young per nest). 18.3% of all chicks were found dead but intact within the enclosure, and hence died likely of other causes than predation. Another 24.2% of all young disappeared without trace before the fledging period.

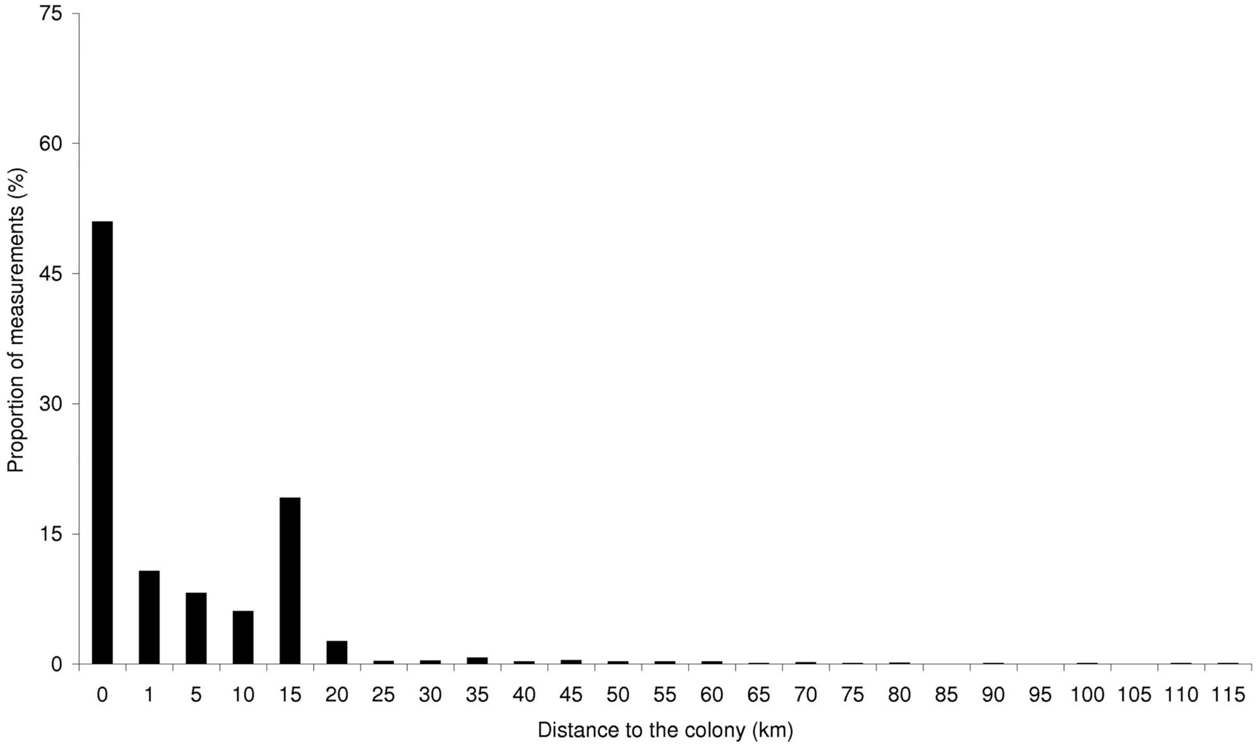

Figure 2. Distance of the GPS measurements (in 5 km categories) measured from the centre of the colony. Category '0' refers to locations in or around (up to 1 km) the colony. The vertical axis shows the proportion of a certain category from all measurements.

Table 3. Overview of reproductive parameters measured inside and outside the enclosure of the Noordplaat. Hatching and fledging success outside the enclosure was not reliably estimable due to chicks leaving the nest and wandering freely around.

	No. nests	Clutch size mean (±sd)	Hatching success %	Fledging success %	No. fledglings /pair
Outside enclosure	21	2.9 (0.3)	–	–	–
Encl. with GPS logger	4	3.0 (0.0)	92	33	1.3
Encl. with colour-ring	4	2.8 (0.5)	91	45	1.3
Encl. control	5	3.0 (0.3)	87	73	2.0
Total enclosure	13	2.9 (0.3)	90	51	1.6

There was no significant difference in the number of chicks died and fledged per adult between the treated and control groups within the enclosure (V-square statistic: df = 1, $\chi^2 = 2.76$, $P = 0.96$). Similarly, the number of hatched eggs and the number of resulting chicks fledged did not differ significantly between the treated and control groups (McNemar $\chi^2 = 3.23$, $P = 0.72$).

Discussion

The results provided insights into the flight patterns, habitat use and foraging site selection of Lesser Black-backed Gulls breeding in a colony 30 km from the coast. Based on the GPS measurements and the diet analysis, we believe that the birds did not forage in the North Sea and subsequently did not rely on marine food sources, as birds breeding in colonies directly on the coast mainly typically do (Garthe *et al.* 1996, Camphuysen 2013). Our research revealed that birds within the enclosure relied on a terrestrial diet, yet still reached a relatively high reproductive output.

Although the sample size was small, the fledging success at Lake Volkerak was high compared with traditional natural sites, such as coastal colonies in the Netherlands (0.49 fledglings/nest; Camphuysen 2013), Sweden (0.02–0.16 fledglings/nest; Lif *et al.* 2005) or England (1.21 chicks/pair; Sellers & Shackleton 2011). The productivity rates we measured are more comparable with that of urban inland nesting Lesser Black-backed Gulls, which might be foraging on similar resources (2–3 fledglings/nest; Rock 2005, Sellers & Shackleton 2011). Also, inland colonies in the Netherlands were shown to have higher reproductive output than that of stable or decreasing colonies on the coast (Spaans 1998b), which likely reach low breeding success and growth rates due to food shortages (Bukacinski *et al.* 1998, Spaans 1998a). Compared with these natural coastal colonies, even the fledging success of our tagged birds (1.3 fledglings per nest) was higher.

Outcomes of the diet analysis correspond with previous indications that Lesser Black-backed Gulls breeding more inland consume predominantly terrestrial food (Camphuysen *et al.* 2005, Camphuysen *et al.* 2010). Nevertheless, compared to results of other studies, the complete lack of marine food items in the diet of Lesser Black-backed Gulls was unexpected (Camphuysen *et al.* 2015). Except for two trips directed to the North Sea, conducted by two different individuals that had just lost their eggs or chicks, all other trips were directed inland. Shortly after these trips to sea, GPS data transmission from these two birds stopped, possibly because they left the colony. Failed breeders in a coastal colony in the Netherlands also performed trips to divergent destinations compared with active breeding birds (Camphuysen 2013, Camphuysen *et al.* 2015).

The bolus analysis and the recorded flight movements corresponded with each other; refuse dumps were one of the most important foraging locations for Lesser Black-backed Gulls of the Noordplaat. In contrast, at a coastal colony in the Netherlands domestic waste materials were found in none of the regurgitated boluses of male gulls and only in 16.7% of boluses from females (Camphuysen 2010). Visits of Lesser Black-backed Gulls to the refuse dump of Bergen op Zoom have already been documented, where they were observed to forage on urban domicile – and organic waste (especially meat waste), and the insects concentrated within (Buijs 1998). During the past decade, the importance of this refuse dump for Lesser Black-backed Gulls has grown (R.-J. Buijs, unpubl. data). However, the gulls also proved their opportunistic feeding character by switching to alternative food resources on Sundays when the refuse dump was closed (compare with Tyson *et al.* 2015).

The pellet analysis, on the other hand, suggested a minor importance of the refuse dump. Food pellets give a representation of the diet of a larger fraction of the colony (approximately a third of all birds), in comparison with the few individuals equipped with GPS loggers. However, pellets contain only the non-digestible part of the food (Barrett *et al.* 2007), while highly digestible food, such as bread or meat collected at a refuse dump, leaves nearly no remains in pellets (Ottoni *et al.* 2009). Moreover, fish consumption based on the number of otoliths in pellets may be underestimated (Barret *et al.* 2007). In this sense, pellets are only representative of the non-digestible matter from the consumed food items. For instance, the large proportion of Moles found in the pellets is remarkable. Moles are known to occur in pellets of Lesser Black-backed Gulls with a terrestrial diet (Camphuysen *et al.* 2005) and in an inland colony in the Netherlands a similar share of Moles was found in pellets (Camphuysen *et al.* 2010). Nevertheless, these proportions in pellets might be biased, due to Mole remains being large and easily recognizable.

The diet analysis and the GPS data both verified the main finding of the study: the gulls from this colony apparently did not forage at sea. While the sample size of birds with GPS loggers was small, the combination of tracking data and diet analysis provide complementary results on foraging site selection in terrestrial as opposed to marine habitats. The relatively high breeding success in this colony could be due to the low breeding density, or an artefact of the position of the enclosure, that is, around the highest concentration of nests. Such concentrations suggest a preferred position within the colony (MacRoberts & MacRoberts 1972a, Savoca *et al.* 2011) that are commonly occupied by higher-quality individuals (Kim & Monaghan 2005). The high breeding success could also be a positive effect of the enclosure itself, by making nests less accessible for ground predators, although a 0.5 m high chicken wire should not pose a serious barrier to most ground predators. Nevertheless, our main message holds also in this case, Lesser Black-backed Gulls do not necessarily need to rely on marine food sources, but may also reach (at least temporarily) high breeding performance by consuming food generally considered of lower quality and labelled as 'junk food' (Oro 1996, Annett & Pierotti 1999, Camphuysen 2013).

Foraging on discards at sea was shown to be advantageous for Lesser Black-backed Gulls compared with feeding on land, due to the higher energetic value of fish (Bolton *et al.* 1992, Spaans *et al.* 1994). The availability of natural prey species, like Herring *Clupea harengus* and Sprat *Sprattus sprattus*, may be crucially important for a high breeding success (Noordhuis & Spaans 1992, Spaans *et al.* 1994). At sea, fishing boats or fish shoals can offer a foraging hotspot for gulls by providing a large amount of readily available food (Camphuysen & Webb 1999, Bartumeus *et al.* 2010). However, due to the high competition levels, this holds only for the more dominant individuals (Hudson & Furness 1989). Moreover, due to their mobility, the location of fish shoals or trawlers is rather unpredictable. For birds breeding farther inland, searching for such food sources would also be preceded by a flight to the sea (in our case 30 km to the coast), with all its accompanying time and energy costs (Weimerskirch 2007), which are especially crucial during the chick-rearing period. Decisions in foraging site selection are not only essential for the individual itself, but also for the offspring; staying longer away for food means a lower prey delivery rate and a lower nest attendance that might lead to higher predation rates (Spaans *et al.* 1994, Bukacinski *et al.* 1998). Therefore, foraging offshore, where Lesser Black-backed Gulls have a mean foraging range of 181 km (Thaxter et al. 2012), can be considered for inland breeders rather risk-prone (Annett & Pierotti 1999, Camphuysen 2013).

In contrast, all of our studied individuals exploited predictable, readily available food sources at inland locations mainly within a distance of 25 km, providing a potentially high prey delivery rate and nest attendance. Terrestrial food sources often involve stationary food supplies and the birds can revisit the same foraging location on repeated occasions. Even for females that might be outcompeted at refuse dumps (Monaghan 1980, Greig *et al.* 1985) and hence need to fly longer distances for food, it still seemed to be worth choosing terrestrial foraging sites. To our knowledge, our study is the first to provide detailed information on the foraging site selection, diet and corresponding reproductive output of a non-coastal Lesser Black-backed Gull colony. Despite the limited sample size of our study, based on our results we expect that other inland-breeding Lesser Black-backed Gull colonies may also primarily focus on terrestrial food sources (Camphuysen *et al.* 2005). In view of the recently accepted European Union ban on discards, more and more Lesser Black-backed Gulls are expected to shift to alternative, likely terrestrial, food sources, eventually accompanied by breeding farther inland (Bicknell *et al.* 2013, Camphuysen 2013). Whether an individual can promptly shift its diet or if the frequency of specialists in a population can slowly transition over time, needs to be investigated in the near future, especially as the number of refuse dumps in the Netherlands has declined in recent decades (Camphuysen 2013). Moreover, in 2014, the European Commission adopted a legislative proposal that aims at phasing out landfilling by 2025 in favour of recycling waste, including bio-waste (European Commission 2014). How many large gulls will find their nutritional needs in such a quickly changing world remains to be seen.

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